

ABNORMAL DENTAL DEVELOPMENT AND ITS SIGNIFICANCE IN DASYURIDS AND OTHER MARSUPIALS

MICHAEL ARCHER
Queensland Museum

ABSTRACT

Abnormal dental developments in dasyurids and other marsupials are described, including supernumerary and lost teeth, divided and fused crowns, abnormal molar crown morphology, and accidents of development including abnormal tooth positions or postures and malocclusion. Instances of ephemeral teeth are also given although these are not regarded as abnormal dental developments. The literature of abnormal dental development in non-marsupials as well as marsupials is briefly reviewed. Premolar number variation is not considered a valid means for determining the position of a possibly suppressed fourth premolar in marsupials. P5 and M5 occurrences are regarded as indications of the proliferative potential of the posterior end of the dental lamina. Some supernumerary teeth are regarded as atavisms. Evidence is given that supernumerary teeth may originate as divided tooth crowns. Fused crowns are probably the result of damage to crowded, developing tooth germs. Some abnormal molar crown variations are also probably the result of antero-posterior compression of the developing tooth germ. Examples are given of abnormal tooth shape and number which may be the result of disease. Some abnormal developments in tooth crown shape and occlusion are more frequent among inbred individuals. Many examples of ephemeral teeth noted are regarded as normal, representing rarely noted vestigial milk-teeth or canine teeth in the process of phylogenetic suppression. Although most abnormal dental developments occur in one tooth only, some occur with occlusal and/or bilateral counterparts. These facts suggest that most single-tooth abnormalities are not genetically determined, in contrast to bilateral and occlusal pair abnormalities which may develop under the influence of a dental morphogenetic field.

Skulls and dentitions of 2990 individuals of dasyurids have been examined, representing many stages of dental development. Observations on non-dasyurids have been more limited. Abnormal developments (i.e. those outside limits given with taxonomic descriptions, as noted for example by Archer 1975) in dasyurids and other marsupials may be placed in three categories: (1) supernumerary or lost teeth, loss not obviously being the result of accident or physical disturbance; (2) morphological abnormalities including misshapen tooth crowns, extra cusps, and composite odontomas; (3) developmental accidents including teeth erupting in unusual positions or postures, tooth loss resulting from physical disturbance or disease, and malocclusion. These categories are not mutually exclusive. For example, a supernumerary molar may also have a morphologically abnormal crown.

This review is based (a) on personal observations of specimens housed in collections throughout

Australia, in the British Museum, and in the American Museum of Natural History, and (b) on literature references. For each abnormality, records from these two sources are listed in separate paragraphs. Literature citations are by author and date except that references to Bateson (1894) are so numerous that they are given only as the case number listed by Bateson (e.g. case no. 366). Catalogue numbers are prefixed by letters as follows: Australian Museum, e.g. AM M4343; American Museum of Natural History, e.g. AMNH109524; British Museum (Natural History), e.g. BM No. 2.9.8.7; Butler collection housed in the Western Australian Museum, e.g. B1944; National Museum of Victoria, e.g. C1009; Fisheries and Wildlife Department of Victoria, e.g. D966; Queensland Museum fossil collection, e.g. F4713; Queensland Museum modern mammal collection, e.g. J23087 or JM169; South Australian Museum modern mammal collection, e.g. SAM M7536; Northern Territory Museum, e.g.

NTM274; Western Australian Museum modern mammal collection, e.g. WAM M2477; Western Australian Museum fossil vertebrate collection, e.g. WAM 68.3.43; Queen Victoria Museum and Art Gallery modern mammal collection, e.g. QVM 1964.1.33.

Literature references to non-erupting teeth or teeth so small they have usually escaped detection in description are mentioned here and although these are not abnormal developments, some further examples are given.

The purposes of this study are twofold. Firstly, to attempt to discover whether 'atavisms' occur at any regular positions suggesting sites of earlier evolutionary losses from a toothrow. Secondly, to describe abnormal structural developments in various populations so that abnormal individuals (e.g. unique fossils like the Fromm's Landing Thylacine, Archer 1971) can be more easily evaluated.

Molar cusp terminology is that used by Archer (1974, 1975). Tooth nomenclature is that used by Thomas (1888). Australian marsupial names are those employed by Ride (1970) and Archer (1975). *Sminthopsis* sp. (a) and (b) refer to two species which will be described elsewhere. New Guinean marsupial names are those employed by Laurie and Hill (1954).

DASYURIDAE

MATERIAL EXAMINED AND NUMBER OF ABNORMAL DEVELOPMENTS: Incidence (in brackets) of abnormalities, other than ephemeral teeth, follows the number of individuals examined in the samples listed below.

Sarcophilus harrisi 17 (3); *Dasyurus hallucatus* 64 (2); *D. maculatus* 33 (1); modern *D. geoffroii* 45 (2); fossil *D. geoffroii* 17 (0); *D. viverinus* 11 (1); *D. albopunctatus* 3 (0); *D. dumalli* 4 (0); *Murexia longicaudata* 2 (0); *Myoictis melas* 3 (0); *Neophascogale lorentzii* 3 (1); *Phascosorex dorsalis* 5 (0); *P. doriae* 4 (0); modern *Dasyurus cristicauda* 24 (2); fossil *D. cristicauda* 574 (4); *Dasyuroides byrnei* 46 (6); modern *Antechinus flavipes* 41 (5); fossil *A. flavipes* 252 (0); modern *A. apicalis* 5 (1); fossil *A. apicalis* 77 (2); *A. stuartii* 10 (0); *A. swainsonii* 10 (0); *A. bellus* 14 (2); *A. macdonnellensis* 38 (0); *A. rosamondae* 10 (0); *A. godmani* 3 (0); *Phascogale tapoatafa*, (in access of) 50 (5); modern *P. calura* 19 (1); fossil *P. calura* 31 (0); *Planigale maculata* 43 (11); *P. ingrami* 33 (1); *P. subtilissima* 7 (0); *P. tenuirostris* 14 (1); *P. gilesi* 5 (0); modern *Sminthopsis murina* 140 (7); fossil *S. murina* 615 (0); *S. ooldea* 13 (1); *S. leucopus* 69 (9); *S. crassicaudata* 143 (7); modern *S. granulipes* 6 (1); fossil *S.*

granulipes 207 (0); *S. psammophila* 4 (0); *S. longicaudata* (modern and fossil) 8 (0); *S. hirtipes* 7 (0); *S. virginiae* 37 (1); *S. macroura* 100 (6); *S. sp.* (a) 7 (1); *S. sp.* (b) 3 (2); modern *Antechinomys spenceri* 30 (1); fossil *A. spenceri* 170 (1); *A. laniger* 12 (0); *Ningaui ridei* 2 (0); and *N. timealeyi* 4 (0).

The number of abnormal dental developments recorded above is certainly an underestimate of the true number because many specimens examined have worn teeth and wear obliterates some morphological abnormalities. Also because fossil specimens examined are generally incomplete, likelihood of detecting abnormal dental developments in individuals is markedly reduced.

TOOTH NUMBER: Adult tooth formula of $\frac{5}{3} \cdot \frac{1}{3} \cdot \frac{4}{4}$ is regarded as structurally ancestral for marsupials in general. In living dasyurids the maximum adult tooth formula is $\frac{5}{3} \cdot \frac{1}{3} \cdot \frac{4}{4}$. In most juvenile dasyurids there is also a molariform tooth, dP4, displaced from the tooth row by the erupting P4. Normally non-erupting tooth rudiments (of milk teeth) also develop ontogenetically, lingual to the incisors and canine in dasyurids (Archer 1974).

In *Mrymecobius* (a dasyuroid considered below with dasyurids) there are eight cheek-teeth in the adult dentition. Tate (1947) suggests that one of these is dP4 which persists together with P4.

SUPERNUMERARY TEETH

INCISORS: *Mrymecobius fasciatus*: Two teeth in position of LI³ (case no. 366); extra incisor on lower right side (case no. 367 and noted by Bensley 1903). *Dasyurus* spp.: Swellings interpreted as tooth germs between I² and I³, in front of I₁, and between I₁ and I₂ in sectioned specimens of *D. maculatus* and *D. viverinus* (Woodward 1896). *Antechinus* sp.: Supernumerary tooth positions in sectioned specimens between I² and I³, between I₁ and I₂, and in front of I₁ and these positions were distinguished from deciduous tooth germs (Woodward 1896). Deciduous teeth associated with all incisors (Archer 1974).

CANINES: *Antechinus flavipes* WAM M7111 small accessory LC¹; *A. minimus* D966 small accessory LC¹; *Sminthopsis crassicaudata* J14376 two teeth at LC¹ position. Supernumerary canines observed in this study may be abnormally enlarged deciduous canine tooth rudiments, such as in *Antechinus* (Woodward 1896, Archer 1974).

PREMOLARS: *Dasyurus geoffroii* WAM M4464 tooth between RP¹ and RP³; *Phascogale calura* WAM M8069 tooth either anterior to LP¹ or between LP¹ and LP³; *Antechinus flavipes* WAM

M7107 tooth posterior to L and RP⁺; WAM M6785 extra RP_x, homology uncertain, appears to be anterior to RP₁; *A. bellus* NTM274 two teeth in LP³ and RP³ positions; *A. apicalis* J1741 tooth antero-lingual to LP¹; WAM 64.10.47 extra P, homology uncertain; *Sminthopsis leucopus* C891 tooth posterior to RP₄.

Dasyurus spp.: Swelling of dental lamina in sectioned specimens of *D. maculatus* and *D. viverrinus*, between P1 and P3, interpreted as rudiments of P2 (Woodward 1896). *Phascosorex dorsalis*: Premolar between LP¹ and LP³ (case no. 386). *Antechinus* sp.: Swelling of dental lamina in sectioned specimen between P1 and P3 interpreted as rudiments of P2 (Woodward 1896).

DP4: *Sminthopsis leucopus* D524 spicule between RdP⁴ and RM¹.

MOLARS: *Sarcophilus harrisii*: Possible occurrences of M⁵ discussed below as divided teeth. Fifth molar (Green 1967). *Dasyurus maculatus*: Five upper left molars and five molars on both sides of lower jaw (case no. 385). Bateson (1894) interprets these as LM⁵ and L and RM₅. I agree with Bateson's interpretation. Thomas (1888) describing same specimen, notes that besides being very small, specimen has asymmetrical squamosal bone.

MISSING TEETH

PREMOLARS: *Dasyurus hallucatus* J16753 missing RP³; *Dasyercus cristicauda* J23101 missing RP₃; *Antechinus minimus* D968, D967 missing RP₄; *Planigale maculata* J10989 missing L and RP³; *Sminthopsis* sp. (a) B1939 missing LP¹ and possibly RP₃.

Antechinus flavipes: In sample of seven specimens, one lacked P₁ (case no. 387).

MOLARS: *Sarcophilus harrisii* WAM 71.10.209 missing all LM⁴.

DIVIDED CROWNS

INCISORS: *Sminthopsis crassicaudata* BM No. 2.9.8.7 L and RI⁴ crowns bicuspid. Roots partly divided.

PREMOLARS: *Dasyurus geoffroii* WAM M4464 RP₃ partly divided. LP₃ has transverse groove; *Dasyercus cristicauda* WAM 68.9.91 LP₃ divided and tooth has three roots; J23098 RP₃ crown tip divided; *Phascogale tapoatafa* WAM M7453 LP₃ crown divided and tooth has three roots; WAM M1338 RP₃ crown divided; *Sminthopsis crassicaudata* J11388 RP₃ tip of crown divided; *S. murina* WAM M1642 RP₄ crown partially divided.

S. leucopus AM M4343 LP³ partially divided; D793 LP⁴ partially divided and has three roots; D741, D458, C10019 RP₃ has partially divided crown.

Dasyurus geoffroii RP₄ partly divided along plane transverse to long axis of jaw (case no. 383).

DP4: *Sminthopsis leucopus* D524 spicule between RdP⁴ and RM¹ may represent split portion of RdP⁴; *S. rufigenis* AM M6562 LdP⁴ crown tip divided.

MOLARS: *Sarcophilus harrisii* QVM 1964.1.201 LM⁴ may be completely divided producing two small teeth.

FUSED CROWNS

PREMOLARS: *Dasyercus cristicauda* WAM 69.6.269 P¹ and P³ crowns fused (an isolated maxilla); *Dasyuroides byrnei* J11510 RP¹ and RP³ crowns fused, sharing one root; *Antechinus bellus* CSIRO (Canberra) CM1141 LP¹ and LP³ fused on point of contact; *Planigale maculata* J10989 RP⁴ and RP³ almost completely fused; *Planigale* sp. J14089 LP¹ and P³ fused at base of crowns; *Sminthopsis murina* WAM M2046 LP₁ and P₃ fused.

ABNORMAL CROWN AND ROOT MORPHOLOGY

INCISORS: *Sminthopsis crassicaudata* BM No. 2.9.8.7 bilobed L and RI⁴.

PREMOLARS: *Sarcophilus harrisii* WAM 71.10.209 grossly abnormal tooth in position of LP³; *Phascogale tapoatafa* WAM M7951, WAM M1338 RP₄ has one root; *Dasyercus cristicauda* WAM 68.9.91 LP₃ has three roots; *Antechinus flavipes* B1814 RP¹ caniniform and also tallest premolar; *Planigale tenuirostris* AM M5438 P₄ two-rooted; *P. ingrami* J7656 LP1*3 have buccal notches or imperfections in cingula; *P. maculata* WAM M420 RP⁴ has extra large cusp posterior to paraconid; *Sminthopsis leucopus* D793 LP⁴ resembles enlarged and divided dP⁴; *S. macroura* AM M4403 RP⁴ has very large antero-lingual cingular shelf; *S. sp.* (a) B1939 tooth posterior to LP₁ (topographic homologue of P₃) morphologically resembles molarized protoconid such as occurs on M₄; *S. murina* WAM M6998 L and RP₃₋₄ possess small postero-lingual cusps.

DP4: *Sminthopsis leucopus* D524 RdP⁴ mildly deformed, possibly result of split-off corner.

MOLARS: *Sarcophilus harrisii* QVM 1964.1.134 M⁴ very small; *Dasyurus geoffroii* WAM M4464 talonids very reduced, trigonids enlarged, particularly M₃; *D. maculatus* J16744 LM⁴ either part of

composite dental odontoma or grossly abnormal; *Dasyuroides byrnei* J11509 L and RM³ ectolophs compressed antero-posteriorly; *Planigale maculata* J16721 small buccal cusp on talonid near base of protoconid; *Antechinus apicalis* unregistered LM¹ paracone slightly displaced, paracrista absent, and extra cusp present anterior to displaced paracone; *A. flavipes* WAM M8092 M² has prominent antero-lingual cusp on flank of protocone; *Sminthopsis macroura* WAM M6903 L and RM¹⁻³ ectolophs compressed antero-posteriorly; J7407 L and RM¹⁻² have conspicuous protoconules; WAM M5701 very large entoconid M₄; WAM M5411 M₄ talonid has lingual cusplules and M₁ has tiny cusp between paraconid and metaconid; J23555 R and LM³ ectolophs compressed antero-posteriorly with buccally displaced parastyles; *S. ooldea* WAM M5888 LM₁ has cusp between paraconid and metaconid and tiny cusp in position of entoconid RM₁₋₃; *S. murina* WAM M2477 L and RM₁₋₃ have large entoconids; SAM M7536 LM₁ has cusp anterior-buccal to paraconid; *S. leucopus* C6343 M¹⁻³ ectolophs compressed antero-posteriorly; C1009 M₁₋₄ have tiny metastylids; AM M4343 M₁₋₃ have tiny entoconids; C9566 L and RM⁴ abnormally shaped; *S. crassicaudata* WAM M373 M₄ talonid tricuspid; *S. sp.* (b) J5459 RM₃ entoconid split transversely; *Antechinomys spenceri* WAM 68.2.265 RM₂ with small entoconid; WAM M2860 M₃ has two tiny cusps in topographic position of entoconid.

Dasyurus spp.: RM⁴ of *D. viverinnus* larger than normal sized LM⁴ (case no. 384). Specimen of *D. maculatus* with supernumerary molars (case no. 384, see above). Bateson interprets (I believe correctly) supernumerary molars as LM₅, LM₅ and RM₅. LM⁴ and L and RM₄ enlarged and morphologically abnormal. Tooth in position of LM⁴ more closely resembles normal M³, and teeth in positions of L and RM₄ both resemble normal M₃.

Abnormal Molar Styler Cusps: *Dasyurus hallucatus* WAM M8085 styler cusp B distinct on L and RM¹; *D. viverinnus* J20413 styler cusp B distinct on L and RM¹; *Phascogale tapoatafa* WAM M2855 styler cusp C occurs between B and D on M¹; WAM M1338 styler cusp C large on anterior flank of D on L and RM¹; WAM M6390 styler cusp anterior to D on L and RM¹; *Neophascogale* sp. AMNH109524 styler cusp D divided transversely on RM¹; *Planigale maculata* WAM M420 prominent styler cusp A on RM¹; J19668 styler cusp C on L and RM¹⁻³; J16722 tiny styler cusp E on M¹⁻³ (uncommon but occurs also in three other specimens); *Sminthopsis* sp. (b) J5173 extra styler cusps between B and D on L and RM¹

and LM²; *S. granulipes* WAM M6062 styler cusp D divided transversely on L and RM¹⁻²; *S. murina* WAM M8652 styler cusp D unusually enlarged on L and RM¹, projecting buccally; *S. leucopus* C6343 styler cusp A on M¹, extra styler cusps between B and D on RM³, and extra styler cusp on M⁴; C9566 L and RM⁴ have two styler cusps each.

ERUPTION AND OCCLUSION

Sminthopsis crassicaudata: WAM M4503 has what appears to be reversed (antero-posteriorly) LP₄. Tooth slightly smaller than RP₄. WAM M4497 shows abnormal occlusion resulting from very short lower jaw. RC₁ bites behind RC¹ and RC¹ occludes with RI₃. LC₁ just passes anterior to LC¹. Upper incisors do not occlude. *Planigale maculata*: J8070 has lower canines, premolars and molars heavily worn, while upper cheek-teeth almost unworn. Reasons unknown. Possible that specimen includes wrongly associated dentary. *Phascogale calura*: WAM M8069 maloccluded. RM¹ rotated out of position. Result is hypoconid of RM₁ opposes, rather than shears anterior to, metacone of RM¹ and protoconid of RM₁ bites into protocone basin of RM¹, rather than anterior to protocone. Specimen also possesses supernumerary left premolar (see above). *Dasyuroides byrnei*: J11433 missing LM¹ while spaces set RM¹ and RM⁴ off from RM²⁻³. Left and right lower molar rows crowded antero-posteriorly so that lower molars on both sides distorted out of position. Teeth maloccluded. J10935 has maloccluded RI² which bites lingual to lower incisors. J11509 maloccluded. LM¹ deflected posterolingually and hypoconid of LM₁ passes over tip of metacone producing abnormal wear facet. LM₂ also distorted. LM₂ protoconid occludes with LM² protocone basin, rather than shearing past it with very large wear facet across LM² protocone and paracone. Series of thirty *Dasyuroides byrnei* specimens (including all noted above) in Queensland Museum were bred in captivity. Comparison of measures of brachycephaly (maximum skull width/maximum skull length) in wild-caught and laboratory-bred individuals indicates higher incidence of brachycephaly in latter. Concurrently, much higher incidence of dental abnormalities such as malocclusion, tooth loss, supernumerary premolars, and antero-posteriorly compressed molars evidenced in laboratory-bred samples (Archer and Vernon in preparation).

DISEASE OR TRAUMA

Dasyurus maculatus: J16744 has complex LM⁴ which may be either composite odontoma or

teratoma, possibly result of disease. *Dasyercus cristidauda*: WAM 69.6.165 dentaries fused at symphysis. *Antechinomys spenceri*: J23103 isolated right dentary has RI_{1-3} , C_1 and M_{2-4} with alveoli for M_1 . No trace of any premolar. Dentary in area where premolars missing has roughened surface. Large abscesses occur beneath M_1 and below posterior root of M_4 . Abscess below M_1 has perforated buccal surface of dentary below alveolar margin of M_1 . Case may be example of partial anodontia following disease. *Sminthopsis crassicauda*: WAM M8082 missing LI_3 , C_1 and P_1 . These possibly lost during life, with alveoli then overgrown by bone.

NORMALLY NON-ERUPTING OR EPHEMERAL TEETH

Dasyurus geoffroii: WAM M6370 rudimentary spicule-like tooth in position of normally absent RP^4 ; *Dasyuroides byrnei* J11435 tiny calcified rudimentary tooth adhering to postero-lingual corner LP_3 . *Dasyurus*, *Myrmecobius*, *Antechinus*: Calcified rudiments or positions for milk-teeth associated with incisors of *Dasyurus* spp., *Myrmecobius fasciatus*, and *Antechinus* (species not given) in sectioned material (Woodward 1896). Milk-tooth rudiments associated with C_1 in *Dasyurus maculatus*, *D. viverrinus*, *Antechinus* sp., and *Myrmecobius fasciatus* in sectioned material (Woodward 1896). *Dasyurus hallucatus*: DP^4 (Tate 1947). DP^4 and P_4 normally absent *Dasyurus* (except *D. dumalli*). *Antechinus flavipes*: Milk-canine tooth rudiments and non-erupting milk-tooth rudiments in association with incisors in sectioned material (Archer 1974). Examples noted above of supernumerary canines may represent abnormal development of normally non-erupting milk-canines.

THYLACINIDAE

Abnormal molar cusps, supernumerary stylar cusps, enlarged basal cingula and proximation of paracone and metacone of upper molar in *Thylacinus* spp. (Archer 1971). *Thylacinus cynocephalus* with four lower premolars (Röse 1892). Calcified but rudimentary tooth in *T. cynocephalus* interpreted as dP^4 (Flower 1868).

PERAMELIDAE

Suggestion of undeveloped incisor tooth position between I^3 and I^4 (Woodward 1896). Similar tooth rudiments in *Perameles* (Wilson and Hill 1897). *Echymipera*: In 22 per cent of skulls, supernumerary upper incisor present (Ziegler 1971). Ziegler interprets this as I^5 which normally present in most other peramelids. In series of six

skulls of *Echymipera rufescens* (J123063–8), no examples of supernumerary incisors or other dental abnormalities. *Isodon obesulus*: J23082 shows morphologically abnormal L and RM_1 . RM_1 has normal talonid. Anterior to this are five principal cusps. Anterior three may represent trigonid. Two large accessory cusps also present on tooth, one (normal on some specimens of *I. obesulus*) anterior to hypoconid on buccal edge of crown and other posterior to possible homologue of protoconid. LM_1 identical except that last mentioned accessory cusp less well-developed. LdP_4 has enlarged antero-buccal cusp, usually homologous with protoconid of molars. This cusp less well-developed in RdP_4 . *Isodon macrourus*: J13743 with RP_3 missing. Position marked by pebbly knobs of calcified tissue not extending above oral epithelium. Much more complex pebbly knobs occur near base of P^4 , surrounding P^3 and surrounding posterior margin of P^1 . L and RP^3 partially resorbed at points around crown. Eroded pit in anterior root of LP^4 . LI^1 missing although reason not clear. J8765 has four upper right premolars. Extra tooth apparently between RP^1 and RP^3 . J21908 has no teeth posterior to R and LC^1 , no right upper incisors, rudiments only of two left upper incisors, and no lower teeth. Gum lines irregular and all post-canine alveoli (if they existed) filled with bone.

PHALANGERIDAE

Trichosurus vulpecula: Variation in occurrence of small teeth between C^1 and P^4 and between I_1 and P_4 (Kingsmill 1962). P^1 variably present (case no. 378). 'Premilk' teeth in association with I^3 in sectioned material (Woodward 1896). J23083 isolated left maxilla without normal P^1 . J23070 isolated right maxilla with abnormal tooth in RdP^4 position. Tooth much larger than normal dP^4 and has unusual lingual cusp. Tooth with unclear morphology projecting buccally. J23080 has RP^4 erupting out of alignment antero-buccal to M^1 . *Phalanger* spp.: *P. orientalis* with LI^3 imperfectly bifid, crown almost completely divided, but root single (case no. 368). Individuals of *P. orientalis*: four upper premolars on one side; one premolar absent; two teeth occur in place of P^1 ; and tooth present between normal P^4 and P^3 (case no. 372–275). *P. maculatus* lacking L and RI^3 (case no. 369). 'Premilk' teeth in incisor and canine region sectioned specimens of *Phalanger* sp. (Woodward 1896).

PETAURIDAE

Pseudocheirus spp.: *P. forbesi* has no I^3 and no P^1 (case no. 371). In present study, *P. peregrinus* skulls

(including 23 dentaries) from caves in Western Australia show following abnormalities and variations: J23076 has incipiently two-rooted RP^1 ; J23078, left maxillary fragment, shows same P^1 condition; J23075 has four left upper premolars, extra premolar either first or second in row, both being simple peg-like teeth. Teeth posterior to I_1 and anterior to P_4 lost but alveoli vary in number from one (J23072) to two (J23074) to three (J23073). J11427 has small calcified tooth adhering to postero-buccal corner of RP^4 . Long posterior root present on this tooth and appears that anterior root broken off. Tooth probably dP^4 , not previously recorded in this group because either lost very early in development or not normally developed to stage of calcified crown. *Schoinobates volans*: J22083 has tiny calcified tooth adhering to antero-lingual tip of RM_1 . No roots apparent. This rudiment may represent dP^4 , previously unrecorded in genus. *Petaurus* sp.: In 25 skulls, two show variations in number of post- I_1 -pre- P_4 teeth (case no. 380). One has four on left side. *Hemibelideus leadbeateri*: J9294 has slightly abnormal L and RM_4 . Entoconids and postero-lingual corners of teeth reduced.

PHASCOLARCTIDAE

Phascolarctos cinereus: In sectioned specimen, small calcified incisor present in front of I_1 and another uncalcified incisor present behind I_1 . Toothgerms for lower canine, two lower premolars, and additional upper premolar present; none attain functional maturity (Woodward 1896). Rudimentary dP_4 (Thomas 1887b). Tooth rudiments noted by Woodward and Thomas probably best regarded as uncommon observations of normally occurring structures. J10023 has two incisors in place of RI^3 . Both resemble normal LI^1 . J8811 has very tiny hypocones on L and RM^{1-4} . Size of protoconule varies in this species, being absent to miniscule in R and LM^{1-3} (e.g. J8811) to conspicuous in same teeth (e.g. J10023). J13278 shows two tiny calcified teeth in shallow sockets on right lower side between erupting RI_1 and RP_4 . First of these immediately posterior to I_1 . Second adpressed to antero-lingual corner of P_4 crown. On left side, same two teeth present but anterior one lost, perhaps during preparation of specimen. J7209 has no L or RM^4 but has L and RM_4 . J5749 has mildly twisted L and R dentary, resulting in malocclusion and abnormal resting position of incisors.

MACROPODIDAE

SUPERNUMERARY TEETH

INCISORS: *Macropus giganteus* J23087 small tooth anterior to LI^3 .

PREMOLARS: *Macropus giganteus* J23089 RP^5 erupting beneath RP^4 ; J23108 LP^x present anterior to P^4 ; J23105 RP^x present anterior to P^4 .

MOLARS: *Macropus giganteus* J23110, J23151, J23135, J23150, J23137, J23120, J23125, J23083, J23085 L and RM^5 ; J23107 L and RM^5 and LM_5 ; J23128 L and RM^5 and $?LM^6$; J23109, J23129, J23130 LM^5 ; J23140, J23134 RM^5 ; *Macropus robustus* J23122 L and RM^5 ; J23117 RM^5 . *Megaleia rufa* J23091 supernumerary between RM^3 and RM^4 ; J23086, J23084, J23152 LM^5 ; *M. sp.* J23115, J23147 RM^5 ; J23136 LM^5 ; *Potorous tridactylus* WAM 70.7.242 LM_5 ; *Bettongia lesueur* WAM 68.10.2 M_5 .

Supernumerary molars in *Peradorcas concinnus* common (Tate 1948, Troughton 1967). *Macropus* spp.: Supernumerary molars, premolars, presence of rudimentary canines, and absence of P_4 (Kirkpatrick 1965). Kirkpatrick (1965) notes frequency of some abnormalities (e.g. presence of paired M_5 on maxillae) to be as high as seven per cent in one species. *Bettongia* spp.: M_5 in *B. penicillata* (case no. 390) and *B. lesueur* (Waterhouse 1846, Thomas 1888). L and RM^5 in two other specimens *B. lesueur* and L and RM^5 and L and RM_5 in *B. gaimardi* (as *B. cuniculus*) (Thomas 1888).

MISSING TEETH

Macropus giganteus J23114 L and RM_4 missing; J23119 L and RM^4 missing; J23133 L and RM_4 missing; J23126 all lower molars missing R side only; J23134 RM_4 missing; *M. robustus* J23117 L and RM_4 missing; *M. sp.* J23123 RM_4 missing; J23144 RM_x missing; J23145 RM_4 missing; J23149 RM_4 missing.

Bettongia spp.: *B. penicillata* molar formula was $M \begin{smallmatrix} 1 & - & 3 \\ - & 5 & \end{smallmatrix}$ (Bateson 1894). LM_4 missing (case no. 389). M^4 . . . is itself often aborted in *Bettongia*, there being then only three molars' (Thomas 1888, p. 105).

ABNORMAL TOOTH MORPHOLOGY

INCISORS: *Macropus giganteus* J23092 L and RI^2 show two pronounced lingual grooves and crowns deflected buccally; J23087 RI^3 has large buccal projection from walls of crown adjacent to incisive groove; J23090, J23153, J23111 RI^3 distorted shape; J23112 L and RI^3 shape abnormal.

MOLARS: *Macropus giganteus* J23083 LM^5 horseshoe-shaped, RM^5 similar but more complex; J23085 LM^5 horseshoe-shaped but RM^5 molariform; J23139 RM^4 peg-shaped, LM^4 mildly abnormal; J23109 LM^5 submolariform with one loph and one cusp; J23131 possible odontoma in crypt buccal to LM ; *M. robustus* J23117 prominent

mesostyles on L and RM³; *Megaleia rufa* J23088 RM² with one major transverse loph, RM⁴ may also be peg-shaped (tooth gone); J23091 abnormal supernumerary tooth between RM³ and RM⁴, three-rooted and tricuspid; J23084 LM⁵ metaloph appears complexly folded; J23068 LM⁵ simple conical cusp surrounded by cingulum; Macropodid, indet., F4713 LM₄ lacks clear homologue of hypolophid.

In macropodids, abnormally shaped teeth relatively more common than in other marsupial families. Abnormalities in shape also different from those found in other groups in that divided cusps and crowns, fused crowns, and buccally compressed crowns extremely rare.

Normal morphological variation in premolars of several modern and fossil species of large macropodids described (Bartholomai 1973, 1974), with view to interpreting variation in fossil species.

VARIATIONS IN ERUPTION AND OCCLUSION

INCISORS: *Macropus giganteus* J23087 RI³ on premaxilla-maxilla boundary; J23092 RI³ positioned near maxilla boundary; J23104 skull distorted and RI₁ occludes with LI³.

PREMOLARS: *Macropus fuliginosus* WAM M6956 R and LP⁴ erupting near buccal wall of maxilla.

MOLARS: *Macropus giganteus* J23132 L and RM⁴ erupted abnormally high in tooth row; J23113 RM³ erupted abnormally high; J23126 all upper R molars erupted abnormally, lower molars missing.

NORMALLY NON-ERUPTING OR EPHEMERAL TEETH

INCISORS AND POSSIBLY CANINES: *Macropus irma* WAM M8127 (basiscranial length 44.3 mm) two tooth rudiments, one antero-buccal to unerupted I¹, other on premaxilla-maxilla boundary; *M. robustus* WAM M6976 (51.4 mm) one tooth rudiment on premaxilla-maxilla boundary; WAM M6137 (62.9 mm) no rudimentary teeth, but socket only just resorbed; *M. fuliginosus* WAM M6588 (50.4 mm) shallow socket present on premaxilla-maxilla boundary; *M. giganteus* J23087 (adult) spicule-like tooth immediately anterior to LI³.

These teeth undoubtedly normal in developing dentitions of many species and no examination of sectioned macropodid material fails to mention them, although not commonly observed in gross skeletal preparations.

Many cases cited of normally non-erupting teeth in macropodids (e.g. Flower 1868, Woodward 1893, Hopewell-Smith and Tims 1911, Tate 1947a, Johnson 1964, Berkovitz 1968c, Bartholomai

1973). Incisors of macropodids normally have deciduous predecessors that resorb without erupting (Kirkpatrick 1969). Normally non-erupting canine develops ontogenetically (Kirkpatrick 1969).

DIDELPHIDAE

Bensley (1906) presented comprehensive analysis of normal and abnormal variations in stylar cusp morphology in species of *Monodelphis* (as *Peramys*), *Marmosa*, *Caluromys*, *Metachirus*, *Chironectes*, and *Didelphis*. *Didelphis marsupialis*: Six right upper incisors (case no. 363). Four right lower incisors (case no. 364). Upper incisor missing from left and right sides (case no. 365). One out of 79 had no R or LM⁴ (case no. 388). RM⁴ larger than LM⁴ (also case no. 388).

STAGODONTIDAE

Didelphodon padanicus: Type specimen (dentary fragment) of this Cretaceous didelphid may have had four premolars (Clemens 1966).

CAENOLESTIDAE

Garzonia patagonica: Specimen of Tertiary *Garzonia* may have supernumerary number of antemolar teeth (Sinclair 1906, Ride 1962, Ziegler 1971).

VOMBATIDAE

Extra calcified (but rudimentary) teeth reported in vombatids (Owen 1840–45, Röse 1893).

EUTHERIANS

Abnormal dental developments in human teeth have received considerable attention. The most important general treatise on the subject is Stones, Farmer and Lawton (1966). Several other papers (not noted in Stones *et. al.*) dealing with general dental abnormalities are: Black (1902), Kraus, Jordon and Pruzansky (1966); to papers dealing with specific abnormalities such as shovel-shaped incisors, Carbonell (1963); double-rooted lower canines, Alexandersen (1963); carabelli's tubercle, Meredith and Hixon (1954); abnormal cusp development in addition to carabelli's tubercle, Kallay (1966); dens in dente, Swanson and McCarthy (1947); and to papers dealing with the genetic nature of dental abnormalities such as Brothwell, Carbonell and Goose (1963), and Hopewell-Smith (1913).

Minor dental abnormalities in some placentals are documented, for example by Allow (1971), Bateson (1894), Berkovitz (1968), Berkovitz and

Musgrave (1971), Chasson (1955), Churcher (1959), Fish and Whitaker (1971), Forsten (1973), Frisch (1963), Garn and Lewis (1963), Hooper (1955), Jones (1960), Hooper (1955), Jones (1960), Mech, Franzel, Karns and Kuehn (1970), Miller and Tessier (1971), Peterson and Fenton (1970), Schitoskey (1971), Spinage (1971), Van Valen (1966, 1964), Wolfe and Layne (1968), Zakrzewski (1969), Ziegler (1971).

Several studies have been made using dental abnormalities in eutherians to interpret factors controlling tooth development. These include Berkovitz (1969), Butler (1963), Gaunt (1967), Gruneberg (1951, 1965), Hitchin (1966), Johnson (1952), Kurten (1955, 1957, 1963, 1967), Stockard *et. al.* (1941), Van Valen (1962, 1970) and Wallace (1968).

DISCUSSION

SUPERNUMERARY TEETH

PREMOLAR NUMBER: Diversity of position in abnormally occurring teeth noted in the present study indicates that some interpretations attempting to clarify the marsupial premolar dental formula are probably unjustified. For example, Thomas (1887) concludes that appearance of a premolar between the first and third premolars represents an atavistic reappearance of a lost marsupial second premolar. This view is not held by Owen (1840–5) or by Ziegler (1971). Ziegler concludes (p. 240) that 'The premolar position vacant in all marsupials is . . . most logically homologized with that of the retained first milk premolar of placentals . . . accordingly, the first three metatherian post canines are . . . designated the second, third and fourth premolars.' Owen (*op. cit.*) believes that premolar teeth are normally lost from the front of the premolar row. However, Bateson (1894 p. 249) after an examination of dental variations in marsupials in general concludes that ' . . . the system elaborated by Thomas breaks down; not because there is any other system which can claim to supersede it, but because the phenomena are not capable of this kind of treatment'. Considering cases noted in the present study, it seems that extra premolars may occur at almost any position in the tooth row, as well as anterior and posterior to the first premolar. In addition, recent ontogenetic studies by Archer (1974), Berkovitz (1968) and others have not supported the suggestion of Woodward (1896) that there is clear evidence for a suppressed premolar position between P1 and P3 in marsupials, nor the view held by Owen (1840–45) or Ziegler (1971) that a similar premolar position has been lost in marsupials anterior to P1.

P5: Development of P5 in dasyurids and macropodids invariably results in a premolariform tooth, clearly indicating that potential for premolar production exists posterior to P4. Production of P5 presumably occurs later than P4 since it erupts later than and posterior to P4. Archer (1974) demonstrates that even before P4 is calcified in *Antechinus*, the dental lamina connections between it and adjacent teeth are already breaking down. Prior to normal breakdown of dental lamina, this tissue is continuous posterior to the canine. For this reason, the extra premolar probably could not result simply from an abnormal posterior extension of the premolar part of the dental lamina. It appears that the P5 tooth family position is established well before the tooth actually develops, posterior to the P4 position and anterior to the dP4 position on the continuous band of dental lamina.

M5: Molars sometimes occur posterior to M4 in macropodids but rarely in other marsupials. However, one case noted above of a *Dasyurus maculatus* specimen with L and RM⁵ and LM₅ is of this kind. It differs in that L and RM₄ resemble a normal L and RM₃. This specimen was, in part, the basis for Bateson's (1894) formulation of the concept of homoeosis in meristic series. This concept is that particular teeth in a series may vary in shape, and come to resemble aspects of adjacent teeth. In macropodids with more than four molars, homoeosis is not clearly evident because the normal macropodid M4 closely resembles the normal M3, and homoeotic variation in M4 would not be as obvious as in dasyurids.

M5 probably develops as an extra tooth family position at the posterior end of the dental lamina (Kirkpatrick 1969). In *Peradorcas*, production of additional molars is the normal condition (see Tate 1948). Obstructions to addition of teeth at the posterior end of the tooth row result from lack of space. This crowding may be, in part, responsible for abnormal shape of many supernumerary teeth. Butler (1956), Gruneberg (1937), and Lefkowitz, Bodecker and Mardfin (1953) have suggested that distortion of tooth germs can produce abnormally shaped teeth. Sofair, Bailit and MacLean (1971) and Stein (1943) note that this is most likely to be the case with posterior teeth of a particular tooth series. 'Normality' of supernumerary molars in macropodids may be due to forward progression of molars and consequent relative freedom from crowding.

PROBABLE ATAVISMS

In some taxa with a dental number reduced below that possessed by close relatives, teeth

occasionally occur in the position of the 'missing' tooth family. Such occurrences appear to be rather regular and should be regarded most probably as atavisms. These would include appearances of teeth in some dasyurids (e.g. *Dasyurus*) at the P4 position, and in some peramelids (e.g. *Echymipera*) at the I⁵ position.

EUTHERIANS

Berkovitz (1969), Johnson (1969), Kurten (1963) and others have presented interpretations regarding supernumerary teeth in various eutherians. Berkovitz (1969) demonstrates the existence of dI⁴ in a eutherian carnivore. He suggests this is evidence for the presence of four incisors in primitive eutherians. Johnson (1969) notes the appearance of M⁴ in a murid rodent and considers that this may be the homologue of the normal eutherian M³ and that in murid rodents the so-called M¹ is actually a persistent dP⁴. Kurten (1963) believes that in one lineage of felids, so-called supernumerary molars at the rear of the dentition represent an atavistic reappearance of a molar previously lost through evolution.

Although many Mesozoic mammals had more than seven molariform teeth (e.g. *Peramus* and *Amphitherium*), there is no particular reason for believing that the abnormal marsupial M5 noted in the present study is an atavistic reappearance of a lost tooth. More probably, these teeth are simply the result of abnormal activation of a potential tooth-producing structure, the posterior end of the dental lamina.

MISSING TEETH

Missing teeth, partial anodontia, or hypodontia noted in the present study occur mostly in the premolar region and only rarely in the molar region. Some instances are presumably due to trauma, others perhaps to disease, while others seem likely to be caused by genetic defects. Stones, Desmond and Lawton (1966) note that anodontia in humans is frequently due to a gene mutation in the X chromosome. Brekhus, Oliver and Montelius (1944) note that there are often clear correlations between tooth absences. For example, loss of M1 is usually correlated with absence of other molars. In the only instances of non-traumatic molar loss noted in the present study, there were other teeth missing including premolars as well as molars. However, the great majority of cases of premolar loss do not involve molar loss.

ABNORMAL TOOTH MORPHOLOGY

DIVIDED TEETH: Divided teeth were found in the present study only among ante-molar teeth. Bate-

son (1894) notes that when teeth are divided, the plane of division is usually transverse to the long axis of the tooth row. This was invariable in examples considered here. A tendency for the divided tooth to be a RP₃ among dasyurids is present. There is also evidence for correlation of divided teeth and supernumerary premolars among dasyurids. In *Dasyurus geoffroyi* (WAM M4464) an extra premolar occurs on the upper right side and the RP₃ has a divided crown. Division of single tooth germs in various stages of development may be one way in which supernumerary teeth are produced.

Concepts of tooth development, as discussed by Butler (1956), do not provide a mechanism for actually dividing established cusps. Rather, a divided crown tip could develop from two centres of suppressed mitosis in the developing tooth germ.

FUSED TEETH: Fused, geminated or connated teeth were found in the present study only among premolars. Fusion may involve only roots or anything up to and including the whole crown. Hitchin and Morris (1966) suggest that actual teeth do not become fused by any other means than by cementum after tooth formation is complete. They present reasons (p. 575) why fusion of tooth germs is unlikely to occur after epithelial contact between teeth is broken and follicles develop around each germ. They suggest (p. 583) that '... primary developmental abnormality in connation is persistence of the dental lamina between the teeth germs.' However, it seems equally plausible that physical trauma could result in ruptured follicles and subsequent fusion of previously separated portions of epithelium. Some fused teeth noted in the present study are also abnormally shaped. Combinations of abnormal features might result from fusion of previously ruptured and adjacent tooth germs. These developmental accidents certainly have no evolutionary significance.

OTHER ABNORMAL MORPHOLOGY: Mis-shapen molars noted in the present study are also often supernumerary teeth. In some cases they may be sub-molariform with part of the tooth, such as a protoloph, resembling a serially homologous structure in an anterior molar. M5 is commonly a tooth of this sort. Horseshoe-shaped and peg-like M5s are also known. Supernumerary molars occurring between other molar teeth are generally not molariform.

Some grossly abnormal molars suggest structurally ancestral cusp patterns. Examples of this may be cited among abnormal macropodid molars which show isolated cusps rather than crests. However, an equivalent number of abnormal

crowns do not suggest structurally ancestral shapes, such as the horseshoe-shaped or peg-like supernumerary molars. Stein (1934, p. 1817) notes that '... from a reasonably large collection of human third molars, different specimens could be selected and arranged in such order as to prove almost any theory of the evolution of the human dentition'. Abnormally shaped non-supernumerary molars are also noted above. Compression is a common abnormality of this kind. This was also noted by Archer (1971) in thylacine teeth. Probably this results from compression of the tooth germ follicle. Gruneberg (1937) and Lefkowitz, Bodecker and Mardfin (1953) have stressed the importance of the follicle in production of normally-shaped teeth. Osborn (1902) notes that increasing brachycephaly of rhinocerotids is correlated with antero-posteriorly shorter but wider molars. Butler (1956) suggests the possibility that this is the result of antero-posterior compression of the tooth germ follicles. In most of the examples given in the present study, antero-posterior molar compression is correlated with brachycephaly, shortening of the molar row, and sometimes malocclusion.

Number of stylar cusps present in dasyurid molars is clearly variable within species, although these variants are generally uncommon and their significance is unclear. Except in *Neophascogale* and *Phascosorex*, there are normally only two conspicuous stylar cusps, st.B and st.D. St.A is not usually distinguishable from st.B. Sometimes, a stylar cusp (or pair) is developed between st.B and st.D, and it has been called here st.C. Stylar cusps may appear posterior to st.D. Some didelphids (considered structurally ancestral to dasyurids) have five stylar cusps. Other didelphids have practically no stylar cusps. Bensley (1906) has demonstrated considerable variation in didelphid stylar cusps. He concludes (pp. 12-13) that although these '... relatively small and subsidiary structures in the molar crown are certain to exhibit signs of variation, they are surprisingly constant in their relations ... they show throughout the family indications of a general type ...'. The same can be concluded for the stylar cusp area of dasyurids. Despite intra-specific variation and even inter-specific modification, the dasyurid basic pattern described above is clear. However, more information about the Tertiary record of dasyurid stylar cusp development is required before the structurally ancestral dasyurid condition can be defined.

ERUPTION AND OCCLUSION ABNORMALITIES

Malocclusion is rare among marsupials but several instances have been described. An example

of exaggerated overbite noted above is similar to examples presented by Stockard et al. (1941) among dogs. They suggest that upper and lower jaw development is under separate genetic control because, for example, in a cross between a Saluki Dog and a Basset hound, the hybrid had a skull of a Saluki-type in length and a dentary of a Basset hound-type in length, resulting in gross malocclusion with the C_1 biting behind the C^1 .

Another case of malocclusion noted in the present study, involves *Dasyuroides byrnei*. A large series of these animals were trapped and lodged in the Queensland Museum's collection (e.g. J10226). Some bred in captivity (Mack 1961) through several generations. Comparison of 30 skulls of animals bred in captivity and the 9 animals caught in the wild indicates that problems of malocclusion and missing teeth occurred only among animals bred in captivity. In addition there was occurrence of abnormally compressed molars and brachycephaly in some animals bred in captivity. Reasons for this are not clear but factors such as diet and inbreeding are likely to have been involved.

ABNORMALITIES AND DISEASES

Examples of morphological variation, tooth loss, and bony accretion around the tooth roots noted in the present study may be the result of disease. In other instances, some teeth show abnormal dentine accretions around roots, and one specimen may possibly represent a composite odontoma. The difference between composite odontomas and congenital teratomas such as ovarian dermoid cysts (Stones, Farmer and Lawton 1966) seems to be one largely of position. The case noted in the present study involves an abnormal M^4 with apparently several surrounding and related calcified structures. There is, however, no evidence that these calcified structures and M^4 were fused.

EPHEMERAL TEETH

Ephemeral teeth observed in sectioned material or carefully prepared juvenile specimens, do not really represent abnormal dental developments in the sense outlined in the introduction. However, they have been considered here either because they are not commonly observed or because they represent teeth previously unobserved.

Observations of the occurrence of small calcified incisors are reported in this paper and by others (e.g. Berkovitz 1967, Woodward 1896), particularly among macropodids. They rarely persist in adults. These teeth probably represent true deciduous teeth related to the incisors (as suggested by Kirkpatrick 1969). Clear embryological evi-

ence for them is known (e.g. Archer 1974, Berkovitz 1968c, Rose 1892, Woodward 1896) for many marsupial groups and they are generally assumed to be rudimentary deciduous teeth. This may not be true for rudimentary canines in macropodids. These may represent rudimentary non-deciduous teeth, which in other macropodids (e.g. potoroines) are parts of the functional adult dentition.

It has been noted that some ephemeral teeth occurring in the position of a 'missing' tooth family in some closely related forms should be interpreted as atavisms. Tate (1947) notes a case of a dental rudiment in the P⁴ region of a specimen of *Dasyurus hallucatus* and considers this a dP⁴. However, its actual identity is doubtful, since it could be either a rudimentary dP⁴ or a rudimentary P⁴. Reduction of size in these teeth is not necessarily correlated. For example, it has been noted above that while the *Phascogale* P⁴ is large, dP⁴ is a mere rudiment (Thomas 1887). In macropodids, while dP⁴ is as large as a molar, P⁴ may be (in some species) a rudiment. This is clearly so in thylacine (Flower 1868), adding support to the idea (Archer 1974, Berkovitz 1966) that the two teeth do not belong to the same tooth family and hence development of one may not depend on development of the other.

Bateson (1894) concludes that meristic variation in teeth is discontinuous, and that a structure was either a tooth or not a tooth. However, ephemeral teeth in the incisor and canine regions clearly present exceptions to this concept. These have been found in all stages of development from mere lingual growths of dental lamina to calcified and even erupted teeth. Commonly, even after calcification, the teeth are resorbed. Sometimes they persist into the adult dentition as do the small canines in some species of macropodine and most potorine macropodids.

DENTAL ABNORMALITIES AS INDICATORS OF PATTERN IN DEVELOPMENT

Value of dental abnormalities in general in understanding factors controlling development of teeth is doubtful. There have been many attempts to interpret the nature of controlling factors by analysis of the kinds and incidence of dental abnormalities.

Butler (1967) concludes, after noting studies of abnormal conditions of human jaws, that disturbances in migration of mesenchyme from the neural crest may account for abnormal developments of teeth and their supporting bones. In cases where the tongue is doubled, a median series of teeth may develop between the two tongues. Similarly in unilateral hypertrophy of the face,

teeth are enlarged on the affected side. It is therefore interesting to consider the possible significance of unilateral and bilateral dental abnormalities. Bateson (1894) finds that dental abnormalities sometimes occur simultaneously on both sides of the head but rarely occur simultaneously in upper and lower dentitions. Nevertheless, he cites examples of extra molars on both upper sides only (e.g. case nos. 178, 179 and 194), on both lower sides only (e.g. case nos. 171 and 251), on upper and lower right sides only (e.g. case nos. 190 and 196), on both lower sides and only one upper side (e.g. case nos. 182 and 385), on both upper sides and only one lower side (e.g. case nos. 166 and 167), and on both upper and both lower sides (e.g. case 189). Similar examples of correlated variations are given for other tooth series and for missing teeth. Apparently all combinations of this sort are possible. In specimens noted in the present study, particularly among macropodids, L and RM⁵ may be grossly different (e.g. J23085) or mirror images of one another (e.g. J23083). The case given of a grossly abnormal L and RM₁ in *Isodon obesulus* shows that complex bilateral abnormalities may occur, without abnormal occlusal counterparts.

Butler (1961, p. 122) considers that 'If the mutation of teeth (upper, lower and adjacent) were fortuitous, variability of pattern would result so frequently in malocclusion that natural selection would operate to reduce that variability to a minimum. Yet molar teeth show a high degree of individual variation.' Accordingly he proposes that genes controlling tooth shape (and presumably number) may have a dual or pleiotropic effect, producing mirror image structures on surfaces of teeth which contact. This idea relates to the concept of dental morphogenetic fields (Butler 1937, and discussed by Butler 1961, Van Valen 1962, 1970, Wallace 1968, *et. al.*). The concept is based on the belief of the equipotential nature of all tooth germs of a particular species (suggested by Bolk 1922). This potential is modified by other factors such as heredity, position in the tooth row, chemical imbalances, disease, trauma, and available room. Many of these factors have been analyzed (e.g. Stones, Farmer and Lawton 1966). However, the way in which position in the tooth row controls tooth shape is not clearly understood. Butler (1967), notes that Remane (1926) figures a specimen of *Colobus* whose first and second permanent molars are dwarfed and premolariform. Stein (1934) notes a specimen of a human M³ which corresponds cusp for cusp, ridge for ridge, and groove for groove with a normal P². These examples suggest that position in the tooth row is

not always the most important factor in development. Butler (1963) regards such variation in dP^3 as evidence for slight shifts in dental morphogenetic field at the molar-premolar boundary, and this may also apply to Remane's (1926) specimen but not to Stein's (1934).

The present study offers no additional examples among marsupials which bear on the question of developmental importance of position in the tooth row. It does provide examples (e.g. bilaterally symmetric abnormal L and RM_1) of abnormal molars that have not been correlated with abnormal occlusal counterparts. It may be that composition of dental morphogenetic fields, if they exist, is much more complex than has been visualized (e.g. by Wallace 1968 and Van Valen 1970).

CONCLUSIONS

Abnormal dental developments do not appear to provide a basis for interpreting position of a supposedly phylogenetic lost premolar tooth in marsupials other than P4 of some dasyurids. It has been concluded elsewhere (Archer 1974) that ontogeny in some dasyurids similarly fails to reveal a 'lost' premolar position in structurally ancestral marsupials. There does not appear to be any sound reason for believing that marsupials phylogenetically suppressed a particular premolar position.

In some dasyurids with only two premolars on each side, there is evidence from dental variations that the P4 position has been suppressed. Such dental variations should be referred to as atavisms.

Abnormal production of P5 and M5 in marsupials suggests that the dental lamina may remain proliferative at its posterior end even after the normal complement of tooth families has been established. This is particularly evident in the macropodid *Peradorcas* where continuous production of supernumerary molars may occur.

Abnormal crown morphology occurs most commonly among premolars. These often exhibit fused or divided crowns. Fused crowns may result from damage to adjacent developing teeth. Divided crowns, because they are sometimes related occlusally to supernumerary teeth, may be one stage in a process in which supernumerary teeth are produced. Abnormal variations are also common on the styler shelf of molars. Grossly abnormal molar crowns are uncommon in marsupials in general but are more common in supernumerary macropodid molars. Distorted molar crowns may result from crowded tooth germs. Among dasyurids, antero-posteriorly compressed molars are among the most commonly encountered molar abnormalities.

Malocclusion and abnormal molar crown morphology appear, among some dasyurids, more common among inbred than among trapped individuals, suggesting some abnormalities may have a genetic basis.

From ontogenetic studies, many ephemeral teeth developing in canine and incisor positions appear to represent short-lived milk-teeth (e.g. macropodid incisors) or small vestiges of teeth in the process of phylogenetic reduction (e.g. macropodine canines). These are sometimes found in dry skulls representing very juvenile individuals, if the skulls are carefully prepared.

Most abnormal dental developments appear to be of little or no significance in interpreting phylogeny, while others do appear significant and suggest that mechanisms determining tooth shape are complex. Dental morphogenetic fields do not always ensure that abnormalities occur with occlusal counterparts and the majority of dental abnormalities occur in one tooth row only. Other examples do involve occlusal or bilateral counterparts, and add support to the concept of dental morphogenetic fields. The apparent inconsistency may be resolved if the majority of dental abnormalities lack a genetic basis.

ACKNOWLEDGMENTS

Dr W. D. L. Ride, as my supervisor, constructively criticised a draft of this work. Dr A. Bartholomai and Mr B. Campbell of the Queensland Museum also provided helpful criticism. Various other people helped by bringing my attention to interesting dental abnormalities including Dr D. Merrilees, Mr A. Baynes, and Ms J. Porter, of the Western Australian Museum, and Dr T. K. Kirkpatrick of the Queensland Department of Primary Industries who also allowed me to study the interesting series of abnormal teeth in his collection of macropodid skulls. Mr K. Thompson, University of Western Australia, kindly donated J23082, the abnormal *Isoodon obesulus*. Dr H. Van Deusen, American Museum of Natural History, Ms J. Covacevich, Queensland Museum, Ms J. Dixon, National Museum of Victoria, Mr B. J. Marlow, Australian Museum, Mr R. Warneke, Fisheries and Wildlife Department, Victoria, Mr P. Aitken, South Australian Museum, Mr S. Parker, formerly of the Arid Zone Research Centre, Mr R. Green, Queen Victoria Museum and Art Gallery, and Dr E. Hill, British Museum, Natural History, allowed me to examine specimens in museum collections. Mr D. Vernon, Queensland Museum, kindly gave me access to records he has kept of the breeding population of *Dasyuroides byrnei* in the Queensland Museum. Mr A. Easton, Queensland

Museum, helped with photography.

While this research was carried out, I received a Fulbright Scholarship, a grant in aid from the American Explorers' Club, and a Research Assistantship to Dr W. D. L. Ride, who was in receipt of a Research Grant from the Australian Research Grants Committee.

LITERATURE CITED

- ALEXANDERSEN, V., 1963. Double-rooted human lower canine teeth. In D. R. BROTHWELL, (Ed.) 'Dental Anthropology'. pp. 235-44. (Pergamon Press: Oxford).
- ALLO, J., 1971. The dentition of the Maori Dog of New Zealand. *Rec. Auckland (N.Z.) Inst.* **8**: 29-45.
- ARCHER, M., 1971. A re-evaluation of the Fromm's Landing thylacine tooth. *Proc. R. Soc. Vict.* **84**: 229-34.
1974. The development of the cheek-teeth in *Antechinus flavipes* (Marsupialia, Dasyuridae). *J. R. Soc. W. Aust.* **57**: 54-63.
1975. *Ningau*, a new genus of tiny dasyurids (Marsupialia) and two new species from arid Western Australia. *N. timealeyi* and *N. ridei*. *Mem. Qd. Mus.*
- BADER, R. S., 1954. Variability and evolutionary rate in the oreodonts. *Evolution* **9**: 119-40.
- BARTHOLOMAI, A., 1971a. Morphology and variation of the cheek teeth in *Macropus giganteus* Shaw and *Macropus agilis* (Gould). *Mem. Qd. Mus.* **16**: 1-18.
- 1971b. *Dasyurus dunmali*, a new species of fossil marsupial (Dasyuridae) in the upper Cainozoic deposits of Queensland. *Mem. Qd. Mus.* **16**: 19-26.
1973. The genus *Protemnodon* Owen (Marsupialia: Macropodidae) in the upper Cainozoic deposits of Queensland. *Mem. Qd. Mus.* **16**: 309-63.
- BATESON, W., 1894. 'Materials for the study of variation treated with special regard to discontinuity in the origin of species.' pp. 1-598 (Macmillan and Co.: London).
- BENSLEY, B. A., 1903. On the evolution of the Australian Marsupialia: with remarks on the relationships of marsupials in general. *Trans. Linn. Soc. Lond.* **9**: 83-217.
1906. The homologies of the styler cusps of the upper molars of the Didelphyidae. *Stud. Univ. Toronto, Biol. Ser.* **5**: 1-13.
- BERKOVITZ, B. K. B., 1966. Homology of the premolar teeth in *Setonix brachyurus* (Macropodidae: Marsupialia). *Archs oral Biol.* **11**: 1371-84.
1967. The dentition of a 25-day pouch young specimen of *Didelphis virginiana* (Didelphidae: Marsupialia). *Arch oral Biol.* **12**: 1211-2.
- 1968a. Some stages in the early development of the post-incisor dentition of *Trichosurus vulpecula* (Phalangerioidea: Marsupialia). *J. Zool., Lond.* **154**: 403-14.
- 1968b. Supernumerary deciduous incisors and the order of eruption of the incisor teeth in the albino ferret. *J. Zool., Lond.* **155**: 445-9.
- 1968c. The early development of the incisor teeth of *Setonix brachyurus* (Macropodidae: Marsupialia) with special reference to the prelaetal teeth. *Archs oral Biol.* **13**: 171-90.
1969. Supernumerary deciduous incisors in the polecat. *Archs oral Biol.* **14**: 863.
- BERKOVITZ, B. K. B. and MUSGRAVE, J. H., 1971. A rare dental abnormality in an adult male orang-utan (*Pongo pygmaeus*); bilateral supernumerary maxillary premolars. *J. Zool., Lond.* **164**: 266-8.
- BLACK, G. V., 1902. 'Descriptive anatomy of the human teeth'. (5th Ed.). Pp. 1-169. (S. S. White Dental Manufacturing Company: Philadelphia).
- BOLK, L., 1922. Odontological essays. 4. On the relation between reptilian and mammalian teeth. *J. Anat., Lond.* **56**: 136.
- BREKHUS, P. J., OLIVER, C. P., and MONTELIUS, G., 1944. A study of the pattern and combinations of congenitally missing teeth in man. *J. dent. Res.* **23**: 117-31.
- BROTHWELL, D. R., CARBONELL, V. M., and GOOSE, D. H., 1963. Congenital absence of teeth in human populations. In D. R. BROTHWELL (Ed.), 'Dental Anthropology'. pp. 179-90. (Pergamon Press: Oxford).
- BUTLER, P. M., 1937. Studies of the mammalian dentition. The teeth of *Centetes ecaudatus* and its allies. *Proc. zool. Soc. Lond. (Series B)* **109**: 1-36.
1956. The ontogeny of molar pattern. *Biol. Rev.* **31**: 30-70.
1961. Relationships between upper and lower molar patterns. *Int. Colloq. Evol. Lower and Non-specialised Mammals, Brussels* **1**: 117-26.
1963. Tooth morphology and primate evolution. In D. R. BROTHWELL, (Ed.) 'Dental Anthropology'. pp. 1-13. (Pergamon Press: Oxford).
1967. Dental merism and tooth development. *J. dent. Res.* **46**, supplement Sept.-Oct. 1967: 845-50.
- CARBONELL, V. M., 1963. Variations in the frequency of shovel-shaped incisors in different populations. In D. R. BROTHWELL, (Ed.) 'Dental Anthropology'. pp. 211-34. (Pergamon Press: Oxford).
- CHASSON, R. B., 1955. Dental abnormalities of the Alaskan Fur Seal. *J. Mammal.* **36**: 562-64.
- CHURCHER, C. S., 1959. The specific status of the new world red fox. *J. Mammal.* **40**: 513-20.
- CLEMENS, W. A. Jr., 1966. Fossil mammals of the type Lance Formation, Wyoming. Part 2. Marsupialia. *Bull. Dep. Geol. Univ. Calif.* **62**: 1-122.
- DANIEL, M. J. and KERSHAW, M., 1964. Recent congenital anomalies in red deer in New Zealand. *J. Mammal.* **45**: 480-83.
- DARWIN, C., 1882. 'The variation of animals and plants under domestication'. (2nd Ed.) Vol. 1: 1-473. (John Murray: Lond.).
- FISH, P. G. and WHITAKER J. O. JR., 1971. *Microtus pinetorum* with grooved incisors. *J. Mammal.* **52**: 827.
- FLOWER, W. H., 1868. On the development and succession of the teeth in the Marsupialia. *Phil. Trans.* **157**: 631-41.
- FORSTEN, A., 1973. Abnormal enamel morphology in fossil equid teeth. *J. Mammal.* **54**: 255-8.
- FRISCH, J. E., 1963. Dental variability in a population of Gibbons. In D. R. BROTHWELL, (Ed.) 'Dental

- Anthropology'. pp. 15-28. (Pergamon Press: Oxford).
- GARN, S. M. and LEWIS, A. B., 1963. Phylogenetic and intraspecific variations in tooth sequence polymorphism. In D. R. BROTHWELL, (Ed.) 'Dental Anthropology', pp. 53-73 (Pergamon Press: Oxford).
- GREEN, R. H., 1967. Notes on the Devil (*Sarcophilus harrisi*) and the Quoll (*Dasyurus viverrinus*) in north-eastern Tasmania. *Rec. Q. Vict. Mus.* **27**: 1-13.
- GRUNEBERG, H., 1951. The genetics of a tooth defect in the mouse. *Proc. R. Soc. (Series B)* **138**: 437-51.
1965. Genes and genotypes affecting the teeth of the mouse. *J. Embryol. exp. Morph.* **14**: 137-59.
- HITCHIN, A. D., and MORRIS, I., 1966. Geminated odontome-connation of the incisors in the dog—its etiology and ontogeny. *J. dent. Res., supplement to no. 3* **45**: 137-59.
- HOOPER, E. T., 1955. Extra teeth in the pygmy mouse *Baiomys musculus*. *J. Mammal.* **36**: 298-9.
- HOPEWELL-SMITH, A., 1913. 'An introduction to dental anatomy and physiology descriptive and applied'. pp. 1-372. (Lea and Febiger: Philadelphia).
- HOPEWELL-SMITH, A. and TIMS, H. W. M., 1911. Tooth-germs in the wallaby *Macropus billardieri*. *Proc. zool. Soc. Lond.* 1911: 926-42.
- JOHNSON, D. H., 1952. The occurrence and significance of extra molar teeth in rodents. *J. Mammal.* **33**: 70-2.
1964. Mammals of the Arnhem Land Expedition. Pp. 427-517. In *Records of the American-Australian Scientific Expedition to Arnhem Land*, Vol. 4, (University Press: Melbourne).
- JONES, J. K., 1960. Absence of third upper premolar in *Eutamias*. *J. Mammal.* **41**: 269.
- KALLAY, J., 1966. Extra cusp formation in the human dentition. *J. dent. Res.* **45**: 1381-94.
- KINGSMILL, E., 1962. An investigation of criteria for estimating age in the marsupials *Trichosurus vulpecula* Kerr and *Perameles nasuta* Geoffroy. *Aust. J. Zool.* **10**: 597-616.
- KIRKPATRICK, T. H., 1965. Studies of macropodidae in Queensland. 2. Age estimation in the grey kangaroo, the red kangaroo, the eastern wallaroo and the red-necked wallaby, with notes on dental abnormalities. *Qd J. agric. Sci.* **22**: 301-17.
1969. 'The dentition of the marsupial family Macropodidae with particular reference to tooth development in the Grey Kangaroo *Macropus giganteus* Shaw'. Unpublished thesis submitted to the Department of Zoology, University of Queensland: 1-128.
- KRAUS, B. S., JORDAN, R. E. and PRUNZANSKY, S., 1966. Dental abnormalities in the deciduous and permanent dentitions of individuals with cleft lip and palate. *J. dent. Res.* **45**: 1736-46.
- KURTEN, B., 1955. Contribution to the history of a mutation during 1,000,000 years. *Evolution* **9**: 107-18.
1957. A case of Darwinian selection in bears. *Evolution* **11**: 412-16.
1963. Return of a lost structure in the evolution of the felid dentition. *Comment. biol. Helsingf.* **26**: 3-11.
1967. Some quantitative approaches to dental micromorphology. *J. dent. Res.* supplement to **46**: 817-28.
- MACINTOSH, N. W. G., and MAHONEY, J. A., 1964. 'A 4,000 years old thylacine tooth (Dasyuridae) from Shelter 2' Appendix 3 (pp. 507-16) In D. J. MULVANEY, *et. al*, Archaeological excavation of Rock Shelter no. 6 Fromm's Landing, South Australia. *Proc. R. Soc. Vict.* **77**: 479-516.
- MACK, G., 1961. Mammals from south-western Queensland. *Mem. Qd Mus.* **13**: 213-29.
- MECH, D. L., FRENZEL, L. D. JR., KARNS, P. D., and KUEHN, D. W., 1970. Mandibular dental anomalies in White Tailed deer from Minnesota. *J. Mammal.* **51**: 804-6.
- MEREDITH, H. V., and HIXON, E. H., 1954. Frequency, size and bilateralism of Carabelli's tubercle. *J. dent. Res.* **33**: 435-40.
- MILLER, F. L., and TESSIER, G. D., 1971. Dental anomalies in Caribou, *Rangifer tarandus*. *J. Mammal.* **52**: 164-73.
- MILLS, J. R. E., 1963. Occlusion and malocclusion of the teeth of primates. In D. R. BROTHWELL, (Ed.) 'Dental Anthropology'. pp. 29-51. (Pergamon Press: Oxford).
- ORINGER, M. J., 1948. Anomalies of human dentition. *Oral Surgery Oral Medicine Oral Pathology* **1**: 1119-30.
- OWEN, R., 1840-5. Odontography. lxxiv and 665 pp. (Hippolyte Balliere: London).
- REMANE, A., 1926. Eine seltsame Gebissanomalie bei einem Stummelaffen, zugleich ein Beitrag zur Frage der Selektionswirkung bei der Gebissdifferenzierung. *Z. Saugetierk.* **1**: 114-20.
- RIDE, W. D. L., 1962. On the evolution of Australian marsupials. Pp. 281-306 in G. W. LEEPER, (Ed.) 'The evolution of living organisms'. (Melb. Univ. Pr.: Melbourne).
1964. *Antechinus rosamondae*, a new species of dasyurid marsupial from the Pilbara District of Western Australia; with remarks on the classification of *Antechinus*. *W. Aust. Nat.* **9**: 58-65.
1970. 'A guide to the native mammals of Australia.' xiv and 249 pp. (Oxford Univ. Pr.: Melbourne).
- RÖSE, C., 1892. Über die Zahnentwicklung der Beuteltiere. *Anat. Anz.* **7**: 639-50 and 693-707.
1893. Über die Zahnentwicklung von *Phascalomys Wombat*. *S.B. preuss. Akad. Wiss.* **38**: 749-55.
- RUSTON, M. A., 1936. Some dilated composite odontomes. *Dent. Rec.* **56**: 766-74.
- SCHITOSKEY, F. JR., 1971. Anomalies and pathological conditions in the skulls of *Nutria* from southern Louisiana. *Mammalia* **35**: 311-14.
- SINCLAIR, W. J., 1906. Mammalia of the Santa Cruz beds, Marsupialia. *Rep. Princeton Exped. to Patagonia* **4**: 333-408.
- SOFAR, J. A., BAILIT, H. L., and MACLEAN, C. J., 1971. A developmental basis for differential tooth reduction during hominid evolution. *Evolution* **25**: 509-17.
- SPINAGE, C. A., 1971. Two records of pathological conditions in the impala (*Aepyceros melampus*). *J. Zool., Lond.* **164**: 269-70.
- STEIN, M. R., 1934. Some variations of the upper third molar. *J. Amer. dent. Ass.* **21**: 1815-9.

- STOCKARD, C. R., *et. al.*, 1941. The genetic and endocrine basis for differences in form and behaviour. *Amer. anat. Mem.* **19**: 367-72.
- STONES, H. H., FARMER, E. D. and LAWTON, F. E., 1966. 'Stone's oral and dental diseases.' (5th Ed.) Pp. 1-1112. (E. and S. Livingstone Ltd.: London).
- SUTTON, J. B., 1890. 'Evolution and disease.' Pp. 1-285. (Walter Scott: London).
- SWANSON, W. F., and MCCARTHY, F. M., 1947. Bilateral dens in dente. *J. dent. Res.* **26**: 167-71.
- THOMAS, O., 1887a. On the homologies and succession of the teeth in the Dasyuridae with an attempt to trace the history of the evolution of mammalian teeth in general. *Phil. Trans.* **178**: 443-62.
- 1887b. On the milk dentition of the koala. *Proc. zool. Soc. Lond.* **128**: 338-9.
1888. 'Catalogue of the Marsupialia and Monotremata in the collection of the British Museum (Natural History).' xiii and 401 pp. (British Museum (Natural History): London).
- TATE, G. H. H., 1947. Results of the Archbold Expeditions. No. 56. On the anatomy and classification of the Dasyuridae (Marsupialia). *Bull. Am. Mus. nat. Hist.* **88**: 101-55.
- 1947a. An example of 'prelacteal incisors' in advanced pouch young of *Macropus*. *J. Mammal.* **28**: 399-400.
1948. Results of the Archbold Expeditions. No. 59. Studies on the anatomy and phylogeny of the Macropodidae (Marsupialia). *Bull. Am. Mus. nat. Hist.* **91**: 233-351.
1951. The banded anteater *Myrmecobius* Waterhouse (Marsupialia). *Amer. Mus. Novit.* **1521**: 1-8.
- TRATMAN, E. K., 1949. An unrecorded form of the simplest type of the dilated composite odontome. *Brit. dent. J.* **86**: 271-5.
- TROUGHTON, E. LE G., 1967. Furred animals of Australia. (9th Ed.) xxxii and 384 pp. (Angus & Robertson Ltd.: Sydney).
- VAN VALEN, L., 1962. Growth fields in the dentition of *Peromyscus*. *Evolution* **16**: 272-7.
1964. Nature of supernumerary molars of *Otocyon*. *J. Mammal.* **45**: 284-6.
1966. Nearly rooted incisors in an abnormal rat, and control of tooth growth. *Evolution* **20**: 428-30.
1970. An analysis of developmental fields. *Devl. Biol.* **23**: 456-77.
- WADDINGTON, C. H., 1966. Fields and gradients. *Symp. Soc. Develop. Biol.* **25**: 105-24.
- WALLACE, J. T., 1968. Analysis of dental variation in wild-caught California house-mice. *Amer. Midl. Nat.* **80**: 360-80.
- WATERHOUSE, G. R., 1846. 'A natural history of the Mammalia'. Vol. 1. Marsupialia, or pouched animals. Pp. 1-553. (Hippolyte Bailliere: London).
- WILSON, J. T., and HILL, J. P., 1896. Observations upon the development and succession of the teeth in *Perameles*; together with a contribution to the discussion of the homologies of the teeth in marsupial families. *Quart. J. micr. Sci.* **39**: 427-588.
- WOLFE, J. L., and LAYNE, J. N., 1968. Variations in dental structures of the Florida mouse, *Peromyscus floridanus*. *Amer. Mus. Novit.* **2351**: 1-7.
- WOODWARD, M. F., 1893. Contributions to the study of mammalian dentition. Pt. 1. On the development of the teeth of the Macropodidae. *Proc. zool. Soc., Lond.* **1893**: 450-73.
1896. On the teeth of the Marsupialia with special reference to the premilk-dentition. *Anat. Anz.* **12**: 281-91.
- ZAKRZEWSKI, R. J., 1969. Dental abnormality in the genus *Castor*. *J. Mammal.* **50**: 652-3.
- ZIEGLER, A. C., 1971. A theory of the evolution of therian dental formulas and replacement patterns. *Quart. Rev. Biol.* **46**: 226-49.